

VI. ON THE CRANIAL ELEMENTS AND THE DECIDUOUS AND PERMANENT DENTITIONS OF TITANOTHERIUM.

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Among other material collected by the Carnegie Museum Paleontological Expedition of 1900 there is a skull and considerable portions of the skeleton (No. 116) of a young *Titanotherium*. This was found near the base of the *Titanotherium* beds about three miles north of the Brewster and Emmons ranch on Warbonnet Creek, in Sioux Co., Nebraska. The skull and lower jaw are of especial interest, since, owing to the immature age of the individual, most of the cranial sutures are still open, making it possible to determine the character of the different bones. Moreover the milk dentition is still preserved, so that it is possible to determine its nature, while the permanent dentition is sufficiently advanced to indicate definitely the method and order of replacement of the deciduous by the permanent teeth.

THE SKULL.

When viewed from above the frontals are much the more conspicuous elements. They are bluntly rounded posteriorly and are projected far backward beneath and between the lateral anterior projections of the parietals. Anteriorly the frontals are continued into two long lateral projections which extend beyond the orbits, overlie the posterior and lateral margins of the nasals and give rise to the pair of horn cores that form such characteristic features in the *Titanotheridæ*. The nasals are arched superiorly, concave inferiorly, with rather long posterior extensions interposed between the frontal horns. In the present specimen the nasals are very thin along their inner margins but much thickened externally and posteriorly, where they give the chief support to the horns. They are slightly shorter than the premaxillaries and somewhat emarginate anteriorly.

The parietals are not so broad as the frontals. They are deeply emarginate anteriorly and posteriorly, where they are separated by the interparietal portion of the supraoccipital much as in *Equus*. From the

above description it will be seen that the anterior border of the parietals overlies and encloses laterally the posterior border of the frontals, while the anterior border of the latter has a like articulation with the nasals, the relative position of these bones being similar to that of the shingles of a roof.

The zygomata are rather broadly expanded and are composed about equally of the malars and squamosals.

When seen from the side the skull appears somewhat low, with an abbreviated facial region and a rather long posterior portion. The occipital crest and anterior frontal regions are each somewhat elevated. The nasals appear rather deep and send down an inferior and posterior projection, which articulates by suture with the superior border of the maxillary. The infraorbital foramen lies wholly within the maxillary. The maxillonasal suture is opposite the middle of the orbit. The lachrymal is rather large. The malar is long and thin, anteriorly it has an extended contact with the maxillary and posteriorly with the squamosal portion of the zygoma. The squamosal rises high above the external auditory opening and overlaps the side of the parietal

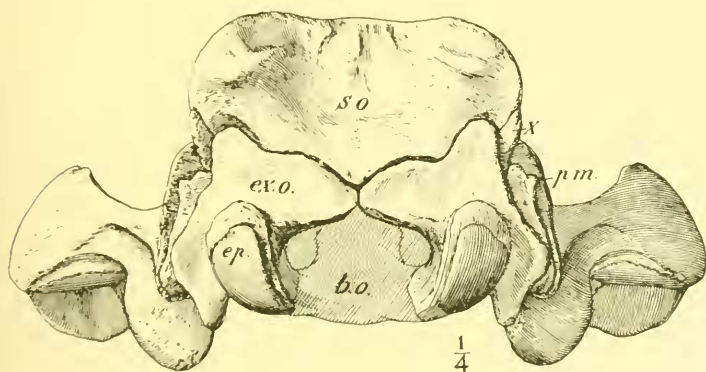


FIG. 1. Posterior view of skull of young *Titanotherium*, one-fourth natural size, No. 116. *s.o.*, supraoccipital; *ex.o.*, exoccipital; *b.o.*, basioccipital; *ep.*, epiphyses of occipital condyle; *p.m.*, paramastoid; *x.*, superior free portion of paramastoid.

throughout most of its length. There is a long, thin, transversely expanded postglenoid process and a shorter and proportionately stronger posttympanic process of the squamosal. The tympanic is absent, having been lost from the present specimen. The periotic is

present and its paramastoid portion appears externally between the posttympanic and paroccipital processes. Just above this there is another small bone which is continued into a long pointed process inserted between the exoccipital and the squamosal and parietal; it probably became coössified later with the periotic, but in the present specimen it is seen as a separate bone, as shown in Fig. 1 and in plate VII. The exoccipitals are rather large and support the paroccipital processes and the occipital condyles. The latter are ossified from two distinct centers, the articular portions bearing distinct epiphyses, as shown in the accompanying figures.

Seen from behind the occiput is low and broad. The condyles are widely separated by the foramen magnum, which is much broader than deep. The condyles are entirely supported by the exoccipitals, which rise and meet in the middle line above the foramen magnum, entirely excluding the supraoccipital from any part in the formation of the superior border of that opening. The supraoccipital is very broad and low. The occipital crest is nearly flat above, but broadly emarginate posteriorly. (See Fig. 1 of the text, and plate VIII.)

Inferiorly the palate is seen to be formed anteriorly by the very short premaxillaries, for the most part broken away in the present specimen, and by the maxillaries, between the posterior lateral extremities of which are inserted the palatines. These form the posterior median portion of the roof of the palate and send backward on either side a lateral projection along the inner sides of the maxillaries and pterygoids, which are continued nearly to the posterior end of the basisphenoid.

The vomers are continued far back as a thin plate resting upon the pre- and basisphenoids and sending downward a thin, knife-like median bony septum. The basisphenoid in the present specimen is entirely free from the basioccipital, the suture being open, and the basioccipital had dropped out and was lost before the specimen was found. The absence of the basisphenoid and tympanic bones makes it impossible to describe and locate the various foramina of this region of the skull.

THE TEETH.

The present specimen is of especial interest in that both the inferior and superior deciduous and permanent dentitions are shown essentially complete.

DECIDUOUS TEETH.

Deciduous dental formula I. $\frac{2}{2}$, C. $\frac{1}{1}$, M. $\frac{4}{4}$ = 28.

Superior deciduous dentition: Deciduous i.₁¹ is slightly smaller than d. i.₂². Both are very small in the present specimen and on the point of dropping out, though their successors have not yet appeared. The canines have not yet pierced the gums, though their crowns are well formed. They are slightly compressed laterally and exhibit distinctly crenulated and rather sharp anterior and posterior margins. Deciduous m.₁¹ is a small tooth fixed in the jaw by two roots, one anterior, the other posterior. The latter is much the stronger of the two. There are two external cusps and one internal cusp. The tooth has been some time erupted and its crown is much worn, but still shows in the middle a small enamel-covered pit, a remnant of a median sinus. Deciduous m.₂² is a rather large tooth but not entirely molariform. The crown is entirely worn away, not a remnant of its structure being preserved. There are two distinct external cones and the small remnant of enamel remaining on the inner border of this tooth exhibits a faint inflection near the middle, indicative of a tendency on the part of this tooth toward the true molariform pattern.

Deciduous m.₃³ is entirely molariform with two distinct external and internal cones. The structure of the crown of this tooth is likewise much obliterated by wear, though not so much as in the preceding tooth. There still persists on the anterior surface a very small enameled pit as a remnant of the anterior valley.

Deciduous m.₄⁴ is the largest tooth of the deciduous series. It is less worn than any of the preceding molars. It is quite molariform and is provided with an external basal cingulum, which character is only faintly, or not at all, developed on the preceding teeth.

Inferior deciduous dentition: The deciduous lower incisors are wanting in the present specimen, having doubtless been shed, or lost, prior to the death of the animal. The alveoles are still faintly discernible. In a second and younger specimen, No. 117, from the same locality, there are two incisors on either side. These have extremely large crowns, are just in process of eruption, and entirely fill the alveolar margin of the premaxillaries between the unerupted canines. Deciduous i.₂² is larger and more advanced than is d. i.₁¹. The canines are in about the same stage as are the superior canines and they do not differ materially from the latter. Deciduous m.₁¹ is a small trenchant tooth

fixed in the jaw by only one root. The crown is composed of two cusps, one anterior, the other posterior. The anterior is the larger of the two. This tooth exhibits only faint traces of wear, and its eruption must have been somewhat subsequent to that of d. m.¹. Deciduous m.₂ is quite molariform, has a very long crown and was fixed in the jaw by two widely separated roots, one anterior and the other posterior. The crown is much worn and anteriorly it is produced somewhat beyond the anterior cusps and forms an additional anterior grinding surface, not seen in the succeeding lower milk molars, nor in the replacing permanent teeth. It was this portion of this tooth that in life was opposed to d. m.¹ and accomplished the erosion already noticed on the crown of that tooth. Deciduous m.₃ is only a little less worn than the preceding tooth and is strictly molariform. Deciduous m.₄ is much larger and less worn than are the preceding teeth. It is in form like permanent molars $\frac{1}{1}$ and $\frac{2}{2}$ and has not the third lobe seen in the last lower molar of all the Titanotheres. The absence of this lobe in this tooth is somewhat remarkable and would seem to form an exception to the general rule *that the last deciduous lower molar in the ungulates has the form of the last permanent lower molar, rather than that of the fourth premolar, which replaces it.* In the present instance this tooth is like the fourth premolar and ms.₁ and $\frac{2}{2}$, and this rule would seem to hold good in the genus Titanotherium, for I have recently examined a number of other jaws of young Titanotheres and find in each instance the same conditions.

THE PERMANENT DENTITION.

Of the permanent dentition in the skull under discussion only ms.₁ are erupted and in position. These teeth are in either instance slightly worn, while ms.₂ are already formed and in position ready for eruption. But ms.₃ are only just commencing to form. The cusps are partially developed, but in each instance they are separated, not having assumed their proper positions in the jaw. Each cusp seems to be developing independently of the others and from different centers, much as certain bones ossify from different centers, which later become connected and form a single bone or tooth as the case may be. In the lower jaw the molars are first formed high up in the ascending ramus just beneath the condyle and base of the coronoid process. From this position, as the jaw lengthens with the growth of the animal, the tooth moves downward and the crown assumes a ver-

tical position, ready for eruption at the posterior end of the horizontal ramus. In this manner $ms.\frac{2}{2}$ and $\frac{3}{3}$ successively occupy similar positions in the ascending ramus. In the present specimen the outer surface of the maxillary and lower jaw have been removed, revealing $pms.\frac{2}{3}$, $\frac{3}{3}$ and $\frac{4}{4}$ in their respective positions. Of these teeth $pms.\frac{2}{3}$ and $\frac{3}{3}$ are the more advanced and in each instance they appear in the act of replacing their respective milk molars. $Pms.\frac{4}{4}$ are not nearly so advanced as the two preceding teeth and appear far below and between the roots of the fourth milk molars, which teeth they will later replace. A somewhat careful examination has failed to reveal any trace of the permanent incisors, canines or first premolars. It is presumable that these teeth will all appear somewhat later, when this region of the skull has been sufficiently elongated to accommodate them.

METHOD AND ORDER IN THE APPEARANCE OF THE DECIDUOUS TEETH AND IN THEIR REPLACEMENT BY THE PERMANENT DENTITION.

A careful study of the comparative degrees of wear shown by the deciduous teeth in Nos. 116 and 117 of our collections shows that they made their appearance in the following order, $d.m.\frac{2}{2}$, $\frac{3}{3}$, $\frac{1}{1}$, $\frac{4}{4}$, $\frac{1}{1}$, $d.i.\frac{2}{2}$, $\frac{1}{1}$, $d.c.\frac{1}{1}$. The canines were just cutting the gums when $d.ms.\frac{2}{2}$ and $\frac{3}{3}$ were ready to drop out.

Of the permanent teeth the superior and inferior first molars were the first to appear, followed a little later by $pms.\frac{2}{2}$ and $\frac{3}{3}$. The next to cut the gums would be $ms.\frac{2}{2}$, which would appear shortly after the second and third premolars. Then, after a considerable interval, $pms.\frac{4}{4}$ would replace deciduous molars $\frac{4}{4}$, and these would be shortly followed, as the jaws increased in length, by molars $\frac{3}{3}$, while the permanent canines and incisors would be the last to appear, but in what order is not determinable from the material at hand.

All the dental and cranial characters above mentioned are well shown in the accompanying illustrations, which have been made from drawings by Mr. Rudolph Weber.

No. 116 has been freed from the matrix and very skillfully mounted as a disarticulated skull by Mr. A. S. Coggeshall, a feat rarely possible in fossil skulls, more especially when they are from so old a formation as the Oligocene.

EXPLANATION OF PLATES.

PLATE VII.

Skull of young *Titanotheres* (No. 116) seen from left side, one fourth natural size, na, nasal; fr, frontal; la, lachrymal; mx, maxillary; pmx, premaxillary; ma, malar; sq, squamosal; pa, parietal; x, free portion of paramastoid; ep, epiphysis of condyle; po, paroccipital process; pm, paramastoid; pt, posttympanic process; pg, postglenoid process. Deciduous and permanent dentitions indicated by the usual symbols.

PLATE VIII.

Superior view of same skull (No. 116) one fourth natural size. iof, infraorbital foramen; ip, interparietal process of supraoccipitals; so, supraoccipitals. Other letters as in Plate VII.